Antarctic Science 9 (2): 121–133 (1997)

Mesoscale distribution and abundance of four pelagic copepod species in Prydz Bay

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Abstract: Knowledge of copepod abundance and distribution has been limited, particularly in the Indian Ocean sector, as the use of coarse sampling gear has meant that copepods were frequently lost from the catch. This study analyses samples obtained from Prydz Bay using a fine mesh (300 μm) Rectangular Midwater Trawl (RMT1) net during summer 1992–93. Results demonstrate that a net of mesh 4.5 mm used in previous studies underestimates total copepod abundance by a factor of 38. The abundance of the smaller species has been underestimated the most. New estimates of copepod biomass indicate that copepods represent approximately 27% of krill biomass. Copepod and krill distributions are shown to be discrete at 82.4% dissimilarity. Mean temperature accounted for 33.6% of the variation in copepod distribution while two of the species showed a slight correlation with chlorophyll *a* pigment data. These results highlight the numerical importance of copepods and the species' distributions in the East Antarctic marine ecosystem.

Received 3 October 1996, accepted 11 March 1997

Keywords: abundance, Antarctic copepods, distribution, Prydz Bay, undersampling

Introduction

The international Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) research program which spanned the 1980s was aimed primarily at assessing krill (*Euphausia superba* Dana) stocks. This bias reflected the commercial importance of krill as a fishery and their widely accepted role as a principal link to higher trophic levels. It is now recognized that other zooplankton provide a link between the primary producers and higher order consumers. To quantify the role of copepods in this link we need to know how much they contribute to zooplankton biomass.

Most zooplankton research in the Southern Ocean, including that undertaken during BIOMASS, has concentrated around the Antarctic Peninsula in the Atlantic sector. However, a few studies have been conducted in the Prydz Bay region of the Indian Ocean sector by Australian (e.g. Hosie & Stolp 1989, Hosie & Cochran 1994, Hosie 1994a, 1994b), Polish (e.g Zmijewska 1983) and Japanese (e.g. Yamada & Kawamura 1986) expeditions. The former Soviet Union also carried out extensive zooplankton studies on community structure in the Indian Ocean sector during the 1970s and 1980s and one paper (Budnichenko & Khromov 1988) is referred to for comparison with this study.

Of these studies only the Australians have used the RMT1+8 net, with the primary purpose of sampling krill. However, this net has been used extensively in the Atlantic sector to sample both krill and copepods as well as other zooplankton (e.g Atkinson & Peck 1988, Atkinson & Ward 1988, Boysen-Ennen & Piatkowski 1988, Atkinson 1989a, 1989b, Atkinson *et al.* 1990). Analysis of copepods sampled by the RMT1 net in the aforementioned studies have shown much higher abundances than estimates from the RMT8 net in the Indian Ocean sector. While the Atlantic sector has been reported as being more productive than the Indian sector, it is also possible that copepods have been undersampled by the RMT8 net.

Siegel (1986) reported the RMT8 undersamples krill less than 20 mm in total body length. Therefore we reason that copepods, which are generally less than 10 mm in length, would also be undersampled, leading to poor estimates of copepod distribution and abundance in the Indian Ocean sector. This paper reports a study of the four dominant Antarctic copepods, *Calanoides acutus* Giesbrecht, *Calanus propinquus* Brady, *Rhincalanus gigas* Brady, and *Metridia gerlachei* Giesbrecht, sampled with the RMT1 net from Prydz Bay in summer 1992–93. The primary aim is to provide a quantitative estimate of copepod abundance from samples obtained with the fine mesh RMT1 net to compare with data obtained from the RMT8. Secondary aims are to compare copepod abundance with that of krill, and to examine any relationship between copepod distribution, the physical environment and phytoplankton abundance in Prydz Bay.

Methods

Sampling

The Prydz Bay study area was defined for the RSV *Aurora Australis* 1992–93 sampling cruise as the area from 60°–78°E, and 65°S to the coast of Antarctica or the Amery Ice Shelf. Sampling sites were located at 30 n mile intervals along thirteen longitudinal transects which were 1.5 degrees of longitude apart (Fig. 1). Samples were collected from 16 January–7 February 1993, beginning in the north-east of the Bay at station 2 and progressing westward, finishing at station 120. Heavy pack-ice (9–10/10 cover) persisted through much of the area, north of Davis station, around Cape Darnley and west of Mawson station (Fig. 1). This caused some course alteration especially along transects 70°30'–72°E.

A Neil Brown Mark 3 CTD (conductivity – temperature – depth) probe was deployed at each sampling site. It measured temperature and conductivity/salinity from 0–200 m depths. No data are available for stations 2 to 46 due to equipment failure. Temperature and salinity values were integrated from 0–200 m to enable comparison with zooplankton data.

Water samples were collected using a General Oceanics rosette sampler containing twelve 5 l Niskin bottles which was deployed at each sampling station (Wright 1987). Samples were taken at 0, 10, 25, 50, 100, and 200 m depths. Chlorophyll *a* pigment (chl *a*) was measured using the HPLC method developed by Wright *et al.* (1991). We measured ice recession (the number of weeks taken for the ice to recede) from the weekly Northern Ice Limit charts 1992/1993 (Navy-NOAA Joint Ice Center, Naval Polar Oceanography Center, Suitland).

At each sampling station, zooplankton were sampled in a 0–200 m oblique downward haul with the RMT1+8 net (Baker *et al.* 1973). The RMT8 has a general mesh size of 4.5 mm with the last 1.8 m of the net being 1.5 mm mesh, and the cod end 0.85 mm mesh. The RMT1 is 300 μm mesh throughout. The RMT1 and RMT8 nets possess nominal mouth areas of 1 m^2 and 8 m^2 respectively when the net mouth is at 45° to the direction of tow and the net is towed horizontally at 2–3 knots (Roe *et al.* 1980).

An electro-mechanical net release and real time depth sensor were mounted above the nets. The nets were opened 10 m below the surface and then closed at 200 m, or within 20 m of the sea-floor in shallower water. The RMT1+8 was equipped with a flowmeter. The effects of the towing speed (an average of 2.5 knots) and trajectory of the net were taken into account in calculating the volume of water filtered. This was calculated using the equations given by Pommeranz *et al.* (1982) assuming 100% filtration. Basic sorting of taxa was carried out on board ship, where *E. superba* and large and fragile zooplankton were removed. Preservation was in Steedman's solution (Steedman 1976). Samples from the RMT8 net were analysed for macrozooplankton (Hosie *et al.* 1997), and the RMT1 samples were analysed for euphausiid larvae, which forms a separate study. Identification was to species level where possible. In the present study we analysed copepods from the remainder of the RMT1 catch.

The numbers of adults and juveniles of each species were counted for each station. A Kott whirling apparatus (Kott 1953) was used to provide a 1/10–1/2 subsample, of approximately 200–700 individuals per sample. The copepodite V and VI lifestages were pooled based on their similar morphology, and juveniles classed as the copepodites I–IV. Total abundance is expressed as the number of individuals of all copepodite stages per 1000 m^3. Wet weights of individual species were also recorded.

Data analysis

Details of the multivariate analysis techniques, as modified from Field *et al.* (1982) and Kruskal & Wish (1978), have been described previously in Hosie (1994a, b), Hosie & Cochran (1994) and Hosie *et al.* (1997). Multivariate analyses were carried out using BIOΣTAT II (Pimental, R.A. & Smith, J.D., 1985 Sigma Soft, Placentia, California). The

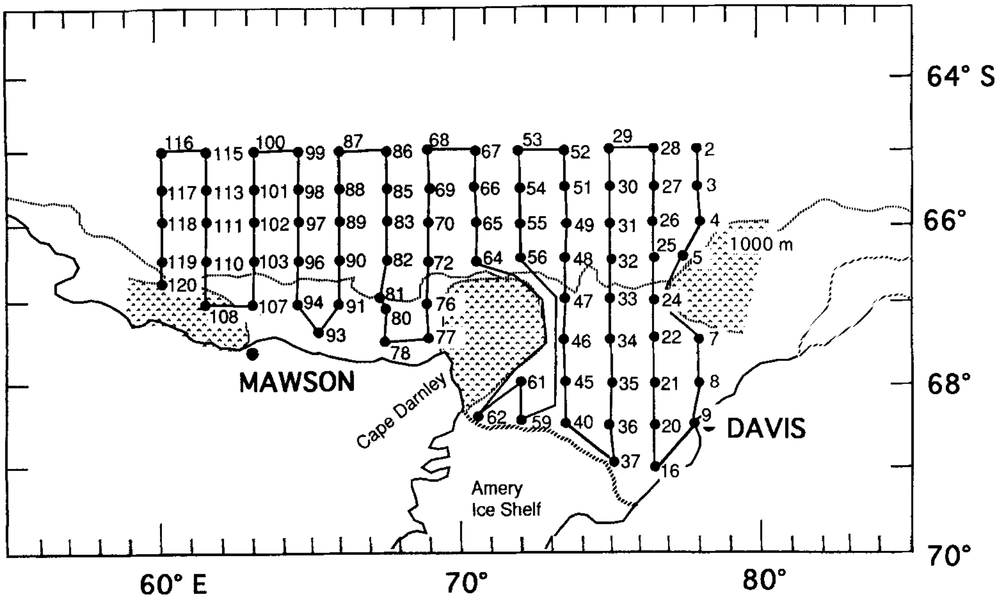


Fig. 1. Cruise track of RSV *Aurora Australis*, 16 January–7 February 1993, showing net sampling sites and the 1000 m water depth contour. Symbols mark areas of heavy pack-ice.

following is a summary of the methodology used in the present study.

Analysis of individual densities in a site by species matrix was made by cluster analysis, using the Bray-Curtis dissimilarity index (Bray & Curtis 1957) and unweighted pair group average linkage, followed by non-metric multidimensional scaling (NMDS) ordination. This determines site associations (community groups) based on similar species composition and was performed on total abundance data. Multiple and simple regressions were undertaken to determine any relationship between the community and individual species with environmental parameters (including chl *a*), and the RMT8 data.

Individual species densities were compared with each of the variables by simple regression, where the abundance (expressed as density) for adults and juveniles of each species were dependent variables and the environmental parameters were independent variables. The species densities were also regressed on the RMT8 copepod data. Stations 101, 113, 115 and 117 had exceptionally high numbers of *R. gigas* which skewed the data set, so they were removed prior to the regression.

Species indicative of community groups were identified by the Student-Newman-Keuls multiple range test (Zar 1984). Species associations were identified by reverse cluster analysis, i.e. a species by site matrix, of the RMT1 copepod and RMT8 krill data. Subsequent ordination was undertaken to verify the cluster analysis. The krill data were removed for the ordination as they formed a group so distinct from the copepods that they compressed the copepod data points against the NMDS vertical axis.

Results

Hydrography and chlorophyll a

Very cold water tends to be found over the shelf region with warmer waters offshore (Fig. 2a). Mean temperature ranged from -1.87°C at Station 61 to +1.28°C at Station 87. A warm water intrusion appeared north-west of Cape Darnley near Station 115. High salinity values are associated with this region of warmer water (Fig 2b). Mean salinity ranges from 33.21 at Station 108 to 34.33 at Station 47.

Three water masses are evident north of the shelf break. The summer surface water (SSW) produces a distinct thermocline at approximately 10–15 m. Below the SSW is the Antarctic winter water (WW) which is typically colder and less saline. The circumpolar deep water is warmer than the WW hence another thermocline occurs between 100–150 m depth.

Values were plotted for each transect to show the mean and peak (regardless of depth) abundance and distribution of primary productivity at the time of sampling. The distribution of mean chl *a* integrated for the upper 200 m is shown in Fig. 3a and the distribution of maximum chl *a* levels in Fig. 3b. Highest chl *a* values were nearest the coast. Phytoplankton concentration based on integrated values from 0–200 m ranged from 0.004 μg chl *a* l^{-1} at station 32 to 1.943 μg chl *a* l^{-1} at station 78. Phytoplankton concentration is generally greater in the transects west of 62°E where values exceed 1 μg chl *a* l^{-1}.

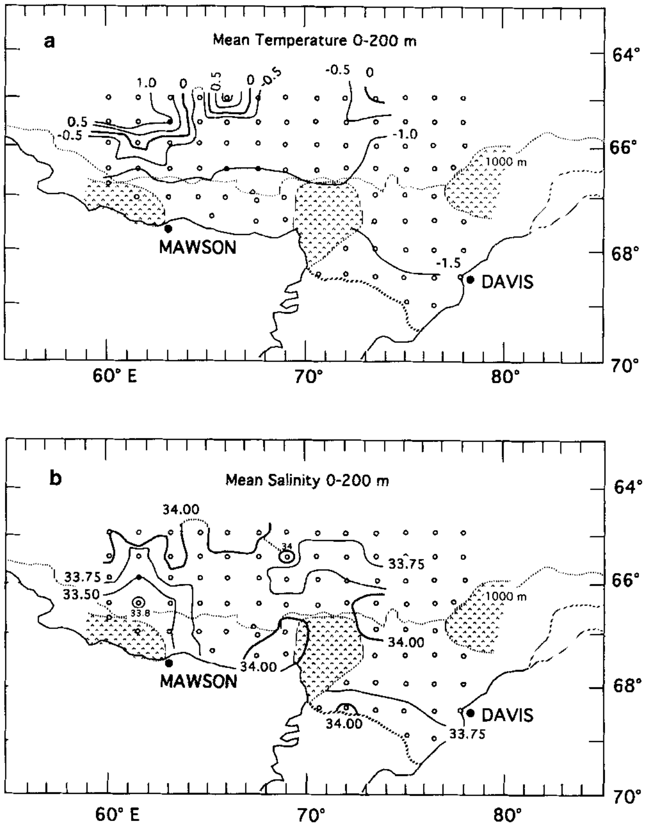


Fig. 2. a. Isotherms of mean temperature (°C) from 0–200 m depth. **b.** Isohalines of mean salinity from 0–200 m depth.

Zooplankton

Maps of species abundance based on the number of individuals 1000 m^{-3} of seawater at each station are shown in Figs 4–7. Overall, species abundance is higher north of the continental shelf edge. *Calanoides acutus* is the most abundant species, followed by *M. gerlachei*, *Calanus propinquus*, and *R. gigas*. However, *R. gigas* juveniles are more abundant than those of *C. propinquus*. In particular the abundance of *R. gigas* adults and juveniles is much greater offshore, with less than 10 ind. 1000 m^{-3} south of the shelf break (1000 m contour line). *Calanoides acutus* shows high abundances along a north-east gradient and is lower in abundance between Davis station and Cape Darnley. To the west of Cape Darnley *M. gerlachei* is distributed widely both offshore and inshore. For all species, adults are in greater numbers than juveniles.

Species densities calculated from the RMT1 net were regressed on values obtained from the RMT8 catch. The

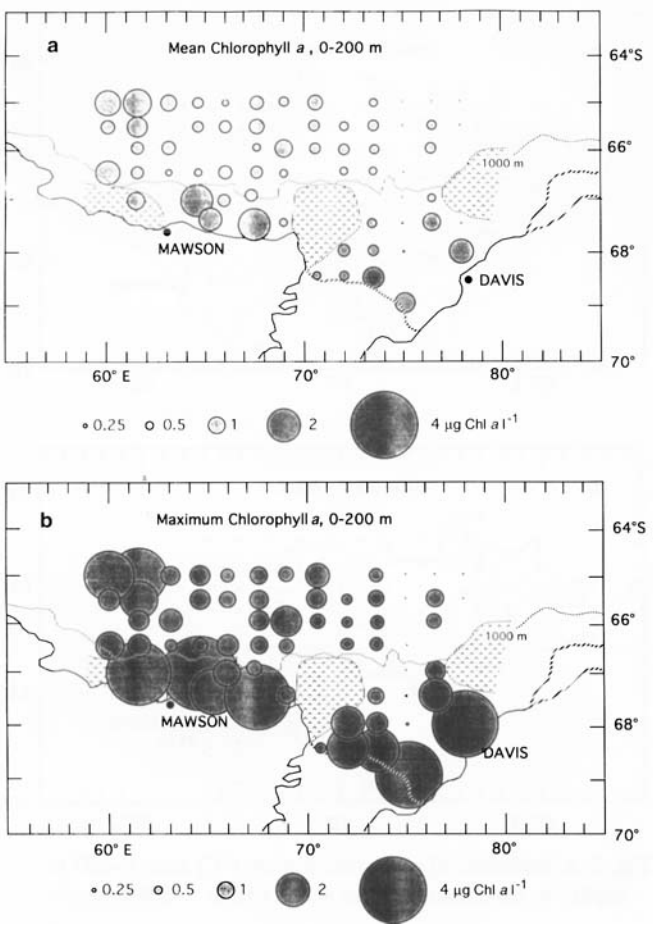


Fig. 3. Distribution of chlorophyll *a* concentrations as µg l^{-1},
a. integrated for the upper 200 m water layer, and
b. maximum chlorophyll values (Hosie *et al.* 1997).

regression coefficients show that *M. gerlachei* abundance is 118 times greater when sampled by the RMT1, followed in decreasing order by *C. acutus*, *C. propinquus*, and lastly *R. gigas* whose abundance in the RMT1 is five times that in the RMT8 (Table I). Note that Hosie *et al.* (1997) used slightly different values to those in Table I in their reassessment of macrozooplankton community patterns based on converted RMT8 zooplankton abundance data. They had used preliminary values obtained from every second transect, whereas Table I values are for all transects.

Comparison of the total copepod density sampled by the two nets shows that the RMT1 catch is 38 times that of the RMT8 while the mean biomass is 11 times greater (Table II).

Table I. Simple regression of RMT1 densities on RMT8 densities for each species. (n = 83).

Species	Regression coefficient	DF	*F* value	*P* value
Rhincalanus gigas	5.2	1, 82	10.5	<.0005
Calanus propinquus	17.0	1, 82	339.0	<.0005
Calanoides acutus	73.1	1, 82	106.2	<.0005
Metridia gerlachei	118.1	1, 82	58.1	<.0005

Table II. A comparison of the density and biomass of *Euphausia superba* and the four copepod species sampled by the RMT8 and the RMT1.

	Euphausia superba RMT8	Copepods RMT8	Copepods RMT1
Mean biomass (g m^{-2})	7.9	0.2	2.1
Mean density (ind.1000m^{-3})	8.8	36.2	1351.5
% Biomass copepod/krill		2.4%	26.6%
Density copepod : krill		4	153

The ratio of copepods to krill based on the RMT8 values is 4:1. However, sampling by the RMT1 shows a ratio of 153:1. The RMT1 copepod biomass was 26.6% of the RMT8 krill biomass.

The 'all life stages' community distribution can be defined by the cluster analysis as four groups at 41% dissimilarity (Fig. 8). Of these four groups the two largest groups (Groups 1 and 3) appear as an oceanic and neritic group respectively and are divided by the continental shelf break (Figs 8a & b). All four species are in significantly high abundance in group 1 (Table III). The three sites (stations 101,113 and 115) which comprise Group 2 contain mostly *R. gigas*. Group 4 consists of stations 9, 20 and 21 which contain very low abundances of *C. acutus* and *C. propinquus*. The adult distribution shows an identical pattern to that of 'all life stages', hence only one distribution map is presented (Fig. 8b). From the cluster analysis, station 93 is classed as belonging to the oceanic group. However, the NMDS plot (Fig. 8c) shows this station grouped with Group 3 (neritic group). The species composition and abundance at this station as well as its geographical location suggests that it is more similar to the surrounding neritic stations than oceanic therefore we accepted the NMDS analysis and included station 93 with Group 3.

The juvenile community distribution contains three outliers (stations 9, 16, and 40). Outliers are samples with a peculiar species composition and thus possess a low similarity to other sites. The aforementioned stations are all adjacent to the ice-edge and contain between one and three individuals only. Four sites (stations 20, 21, 35 and 36) are devoid of any juveniles and therefore are 100% dissimilar to the remaining stations. These sites as well as the outliers were removed for

Table III. Mean abundances, and analysis of variance (*F*) of the four species in cluster groups defined in Fig. 8a. Analyses were performed on $\log_{10}(x+1)$ transformed abundances (Zar 1984). Abundance values shown are the arithmetic mean number of individuals per 1000 m^{-3}. For ANOVA *P* values, degrees of freedom = 3, 79. All are significant to $P<0.0005$. Individual species' abundance in the cluster groups was determined by the SNK multiple range test.

Species	Group 1 Mean	Group 2 Mean	Group 3 Mean	Group 4 Mean	*F*
Calanoides acutus	1255.18	23.73	45.57	0.72	81.32
Metridia gerlachei	356.65	2.57	21.52	0	31.10
Calanus propinquus	184.00	0.97	2.34	0.38	25.50
Rhincalanus gigas	139.31	121.41	0.83	0	42.80

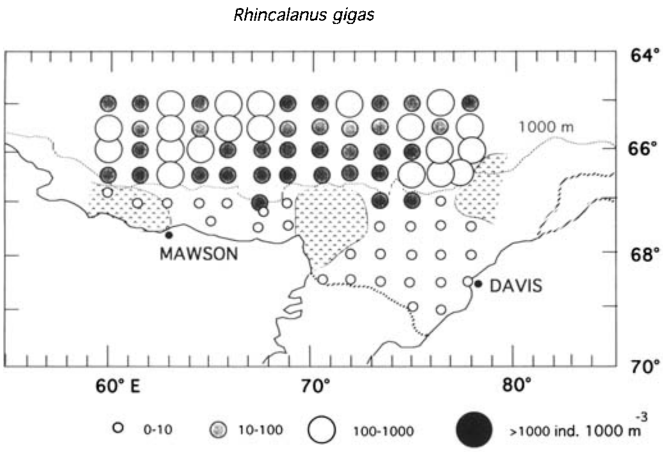


Fig. 4. Total abundance of *Rhincalanus gigas* 'all life stages'. Abundances are expressed as individuals 1000 m^{-3}. The 1000 m water depth contour marks the shelf break.

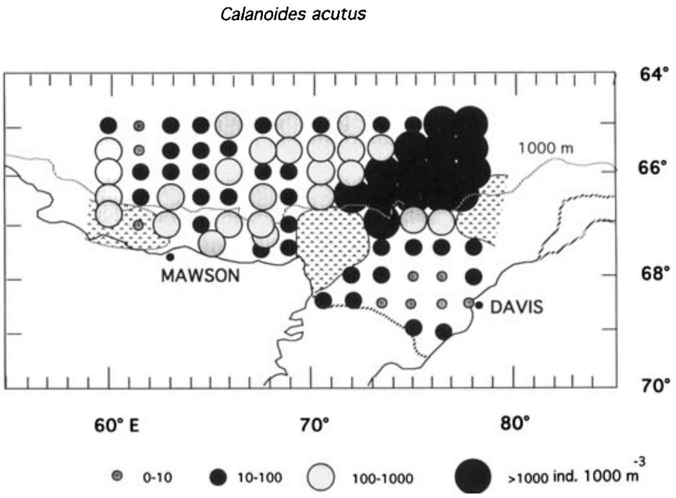


Fig. 5. Total abundance of *Calanoides acutus* 'all life stages'. Abundances are expressed as individuals 1000 m^{-3}. The 1000 m water depth contour marks the shelf break.

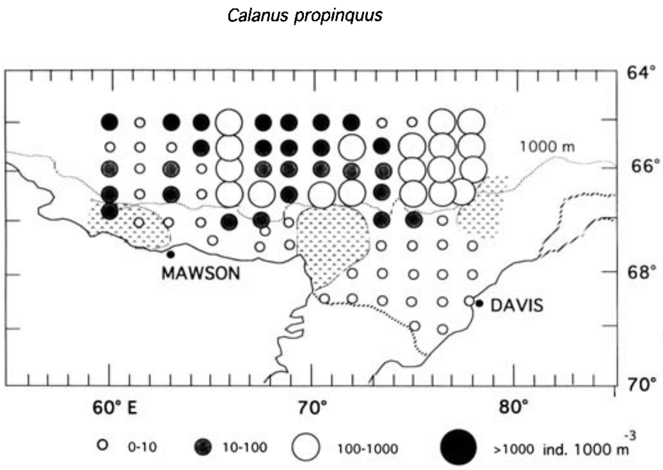


Fig. 6. Total abundance of *Calanus propinquus* 'all life stages'. Abundances are expressed as individuals 1000 m^{-3}. The 1000 m water depth contour marks the shelf break.

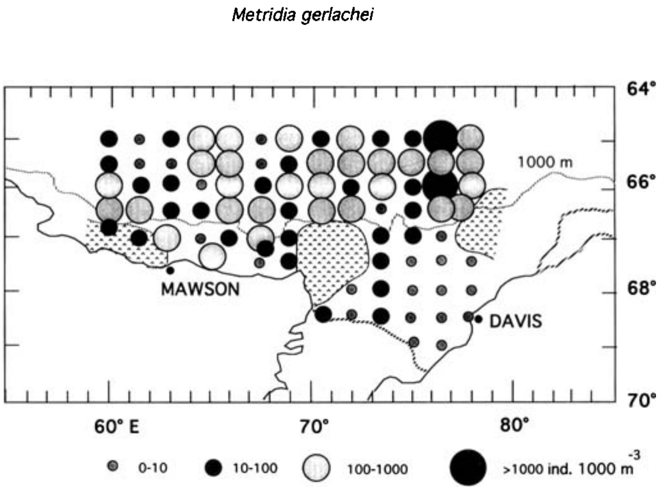


Fig. 7. Total abundance of *Metridia gerlachei* 'all life stages'. Abundances are expressed as individuals 1000 m^{-3}. The 1000 m water depth contour marks the shelf break.

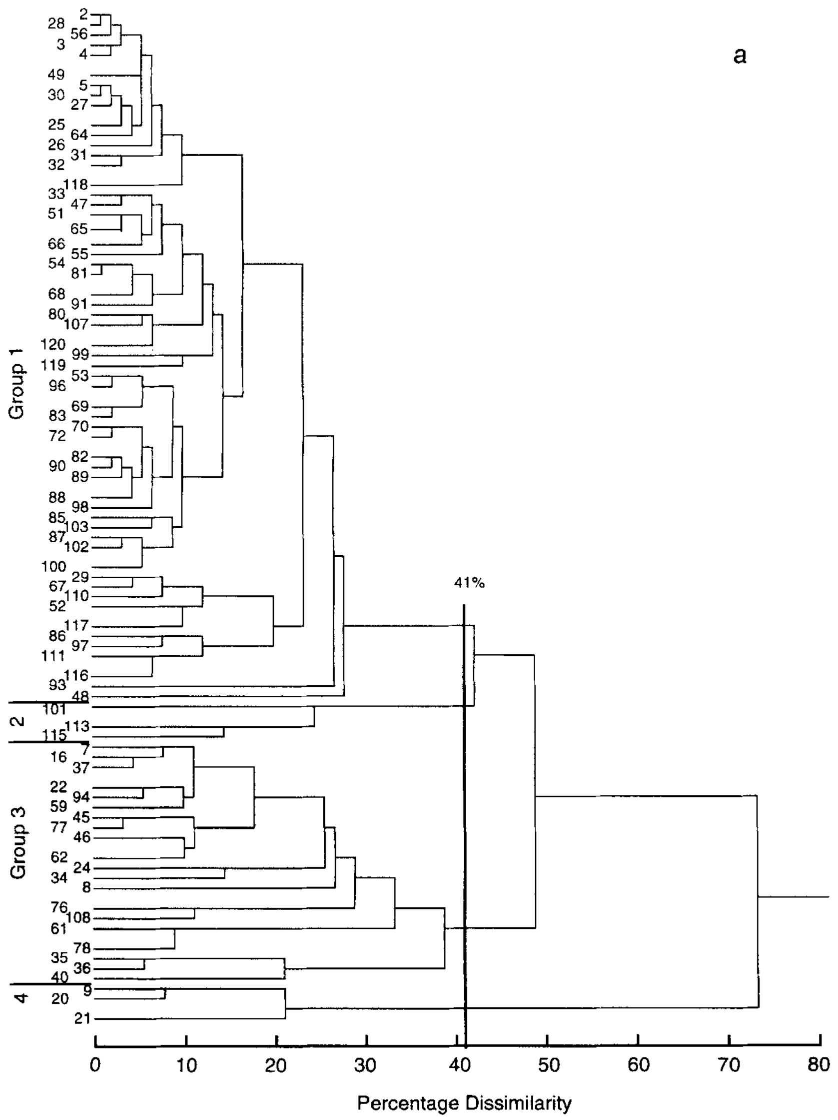
ordination as they can bias results by dominating or compressing other data points especially in subsequent ordination plots (Gauch 1982).

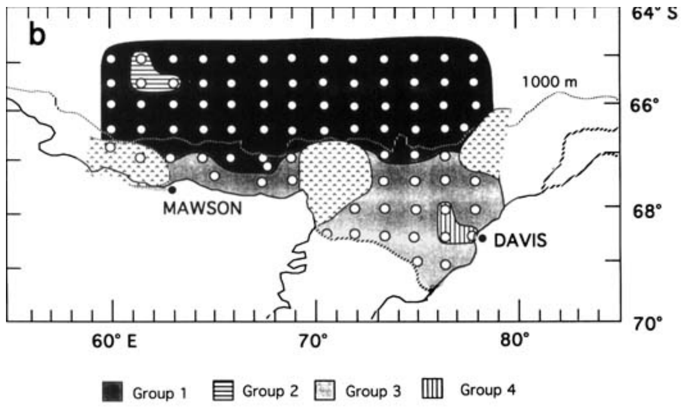
The juvenile distribution shows four groups at 41% dissimilarity. Group 1 defines the oceanic group and Group 4 the neritic group. Group 2 contains 13 sites which have a high abundance of *M. gerlachei* and *C. acutus* inshore and around the pack ice associated with Cape Darnley (Figs 9a & b). Three sites (stations 52, 65 and 99) are offshore sites which are all low in species abundance and comprise Group 3. The juvenile NMDS plot (with outliers removed) confirms these groups and shows stations 34 and 24 as belonging to Group 1 (oceanic group) as defined by cluster analysis, but also as belonging to Group 2 (Cape Darnley) (Fig. 9c).

Environmental data

Table IV shows which environmental parameters are significantly correlated with the cluster groups based on the NMDS ordination scores. The adjusted R^2 value shows the percentage of variation in the data accounted for by the environmental parameter (Jongman *et al.* 1987). Mean temperature is the only significant environmental parameter and accounts for 33.6% of the variation in the data.

Rhincalanus gigas (adults and juveniles) are correlated with temperature and with ice recession but only the juveniles are positively correlated (at low significance) with mean salinity. Abundances of *C. propinquus* (adults and juveniles) and *C. acutus* adults are negatively correlated with chl *a*. (Table V).





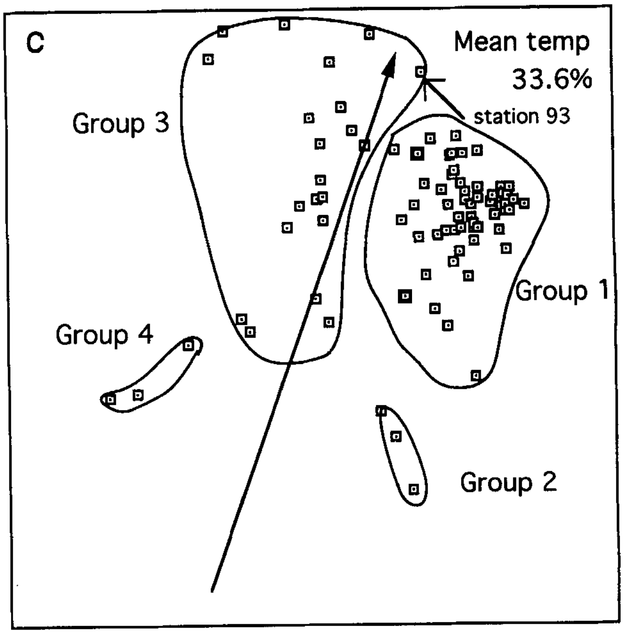


Fig. 8. Distribution patterns for 'all life stages' of the four copepod species. **a.** dendrogram of cluster analysis comparing zooplankton species composition at each sampling site using Bray-Curtis dissimilarity index with UPGMA linkage, after $\log_{10}(X+1)$ transformation of species abundance data. **b.** geographical distribution of station groups defined by cluster analysis shown in Fig. 8a. **c.** Ordination plots of the comparison of sampling sites using non-metric multidimensional scaling and Bray-Curtis dissimilarity index. Respective cluster groups identified in Fig. 8a are superimposed. Significant multiple regression between the ordination scores and the environmental parameters is shown, as well as the fraction (%) of variance in the zooplankton data explained by the parameter (see Table IV). For further detail see Hosie (1994a, b) and Hosie & Cochran (1994). Axis scales are relative in NMDS, based on non-metric ranking of dissimilarity, and therefore are not shown. Stress value = 0.09.

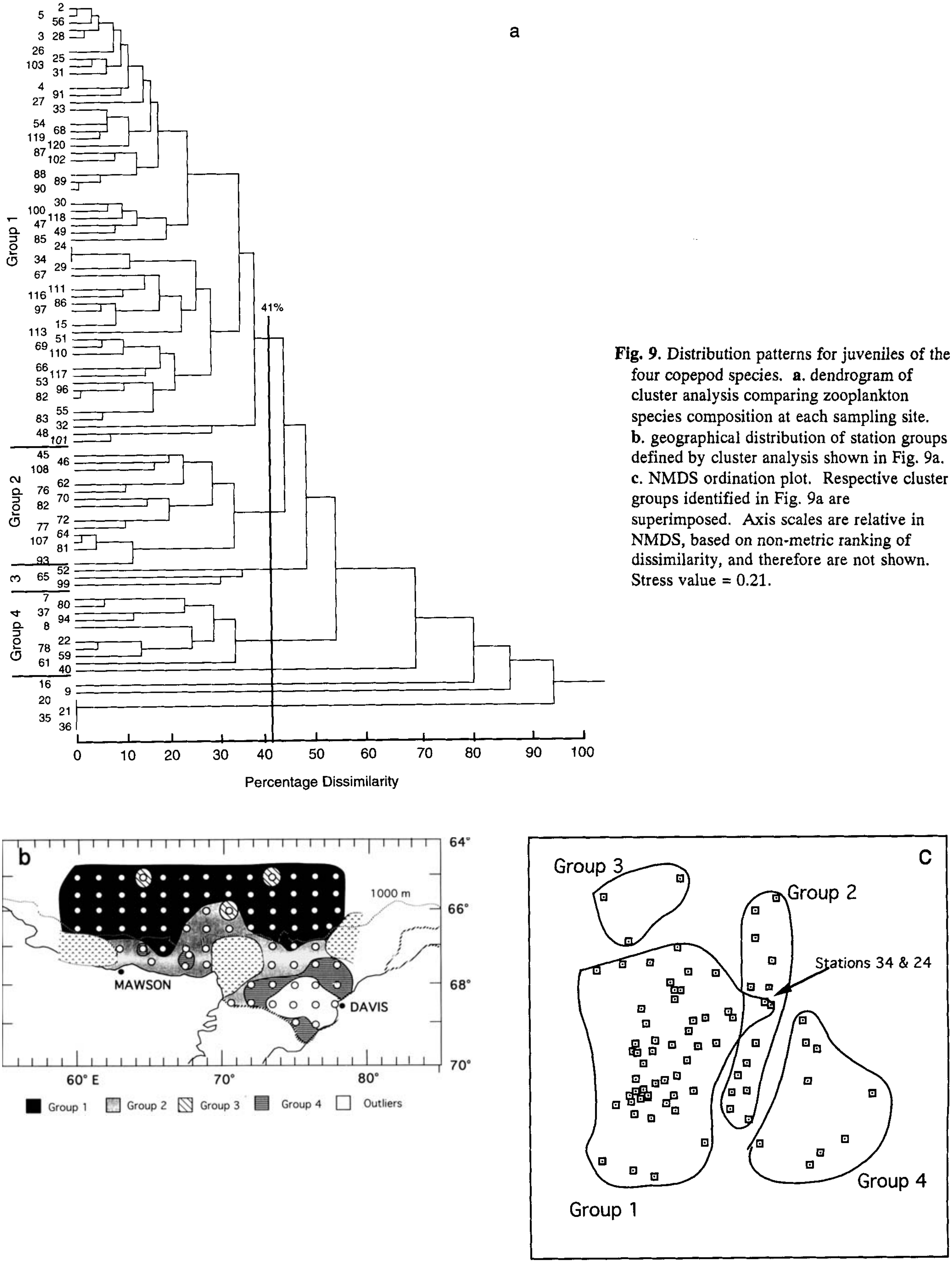
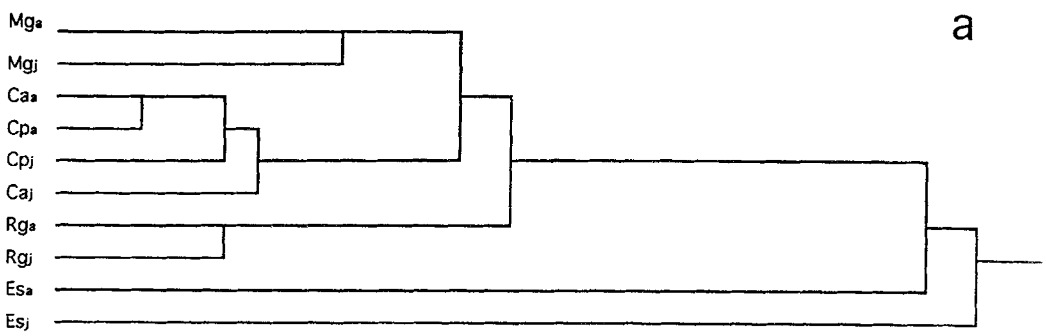


Fig. 9. Distribution patterns for juveniles of the four copepod species. **a.** dendrogram of cluster analysis comparing zooplankton species composition at each sampling site. **b.** geographical distribution of station groups defined by cluster analysis shown in Fig. 9a. **c.** NMDS ordination plot. Respective cluster groups identified in Fig. 9a are superimposed. Axis scales are relative in NMDS, based on non-metric ranking of dissimilarity, and therefore are not shown. Stress value = 0.21.



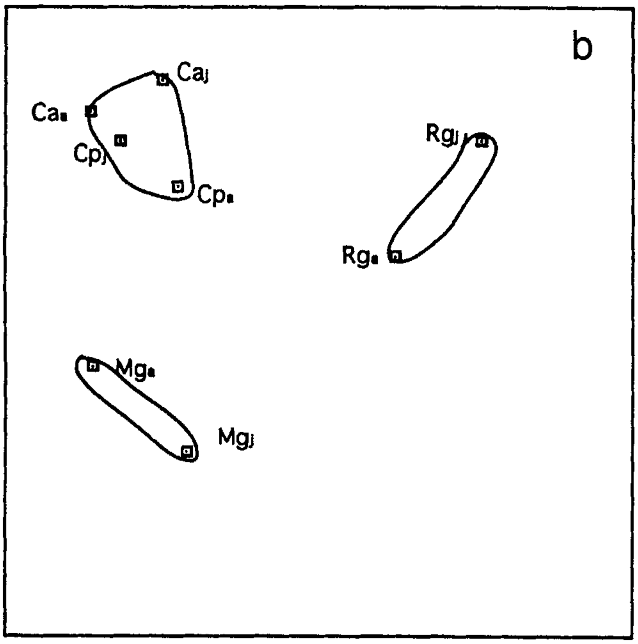


Fig. 10. Species associations of adults and juveniles of copepods and krill. **a.** dendrogram of the inverse cluster analysis comparing species, using Bray-Curtis dissimilarity index with UPGMA linkage, after standardizing species abundance (Hosie 1994a, b, Hosie & Cochran 1994). **b.** NMDS inverse ordination plot comparing dominant species. The *E. superba* data were removed prior to ordination. Respective cluster groups identified in Fig. 10a are superimposed. Axis scales are relative in NMDS and therefore are not shown. Stress value = 0.08.

Mga = *Metridia gerlachei* adults, Mgj = *Metridia gerlachei* juveniles, Caa = *Calanoides acutus* adults, Caj = *Calanoides acutus* juveniles, Cpa - *Calanus propinquus* adults, Cpj - *Calanus propinquus* juveniles, Rga - *Rhincalanus gigas* adults, Rgj - *Rhincalanus gigas* juveniles, Esa = *Euphausia superba* adults, Esj = *Euphausia superba* juveniles.

Copepod and krill associations

Comparisons of krill and copepod density from the RMT1 and RMT8 catches were made. Krill and copepod biomass was also compared based on wet weight measurements. Inverse cluster analysis shows that the euphausiid adults and larvae are 82.4 % dissimilar to the copepod groups (Fig. 10a). Three copepod groups are determined at 52.2% dissimilarity. *Metridia gerlachei* adults and juveniles form one such group, *R. gigas* adults and juveniles form another, and the two

Table IV. Multiple regression analyses between environmental parameters and NMDS scores for two-axis ordination of sampling sites. Regression weights are derived according to Kruskal and Wish (1978). AdjR^2 = Adjusted coefficient of variation which gives the fraction of the variance accounted for by the explanatory variable (Jongman *et al.* 1987). For ANOVA $P < 0.0005$ for those significant variables (in bold).

Variable	Direction Cosines (Regression weights) X	Y	Adj R^2	F value	d.f.
Mean temp	0.3409	-0.9401	**33.61%**	14.6659	2, 52
Ice recession	-0.6935	0.7204	9.70%	5.4056	2, 80
Surf chl *a*	-0.2468	-0.9691	7.99%	3.5190	2, 56
Mean SAL	0.1754	-0.9845	4.82%	2.3688	2, 52
Peak chl *a*	-0.7467	-0.6652	2.46%	1.7678	2, 59
Integr chl *a*	-0.5272	-0.8497	0.14%	0.9584	2, 58

Table V. Significant R values for simple regression of environmental variables on individual adult and juvenile densities of each species. F probability < 0.05. Mg - *Metridia gerlachei*, Ca - *Calanoides acutus*, Cp - *Calanus propinquus*, Rg - *Rhincalanus gigas*.

Variable	Mean T	Mean SAL	Integ chl *a*	Surf chl *a*	Peak chl *a*	Ice Recession
Mg adults	-	-	-	-	-	-
Ca adults	-	-	-0.3336	-0.2893	-0.3179	-
Cp adults	-	-	-0.3150	-0.2893	-0.3272	-
Rg adults	.4733	-	-	-	-	-0.2390
Mg juvs	-	-	-	-	-	-
Ca juvs	-	-	-	-	-	-
Cp juvs	-	-	-0.2829	-0.2773	-0.2855	-
Rg juvs	0.3742	0.2693	-	-	-	-0.2899
n =	55	55	61	59	62	83
DF	1,53	1,53	1,59	1,57	1,60	1,81

species of the Calanidae family *C. acutus* and *C. propinquus* adults and juveniles form the third group. The ordination plot verifies these groups, showing the adults of each species (including the Calanidae species) grouped with their respective juveniles (Fig. 10b). Note that *E. superba* data were removed prior to ordination.

Discussion

Abundance and biomass

Analysis of copepods from the RMT1 catch shows much higher abundances than previous estimates determined from the RMT8 catch in Prydz Bay. The coarse RMT8 net has underestimated the total density of copepods in this region by 38 times. While *R. gigas* was under-sampled by a factor of five, *M. gerlachei* was under sampled by a factor of 118.

At stations 101, 113, 115, and 117, the number of *R. gigas* individuals in the RMT8 catch was greater than the RMT1. These values were removed as extraneous counts. The two most probable causes for this high abundance are either that the net did not sample properly, or that the RMT8 encountered an aggregation of *R. gigas* individuals missed by the RMT1. Given that the net appeared to sample adequately for surrounding stations, we suggest aggregation as the cause of this anomaly.

Of the four species, *C. acutus* is overall the most abundant copepod in Prydz Bay, followed by that of *M. gerlachei*, *C. propinquus* and *R. gigas*. Juvenile abundance shows a similar trend but *R. gigas* abundance is greater than *C. propinquus*, possibly due to its protracted and later spawning period and overall different life-cycle (Atkinson 1991). *Calanoides acutus* juveniles were in greatest abundance and Schnack-Schiel &Hagen (1994) likewise report high numbers of *C. acutus* juveniles in early summer. These patterns of abundance agree with results from Zmijewska (1983) which show that during summer in Prydz Bay *C. acutus* was more abundant, than *C. propinquus* and *M. gerlachei*, followed by *R.gigas*. Previous abundance estimates using the RMT8 net in Prydz Bay, however, indicate that *R. gigas* is one of the most abundant species (Hosie &Stolp 1989, Hosie *et al.* 1997). Our findings now show that this is a sampling artefact.

Table VI compares our data with that of previous studies in the Prydz Bay region and clearly shows that the RMT8 has consistently undersampled copepods. Our results are lower than those studies which used nets of similar mesh size to the RMT1 and sampled at similar depths (Zmijewska 1983, Yamada & Kawamura 1986, Atkinson 1989b). We deduce that this is because the sampling sites in these studies were located further offshore and copepod abundance is reported to be higher offshore (Budnichenko & Khromov 1988, Hosie & Cochran 1994). Variations in the time of sampling, e.g. early vs late summer, can also affect total abundance due to the seasonal effect on the life-cycles of individual species (Boysen-Ennen & Piatkowski 1988, Atkinson 1991).

Copepods dominate the non-euphausiid zooplankton biomass in the open ocean (Voronina 1968) and Conover & Huntley (1991) suggest that their biomass is at least equal to, if not greater than that of krill. Estimates in East Antarctica by Hosie *et al.* (1997) sampling with the RMT8 net, suggest that copepod biomass accounts for only 2.4% that of krill. However, based on our estimates from the RMT1, copepod biomass appears to be much more significant, equivalent to more than one quarter of the krill biomass. While the RMT1 total copepod density (number of individuals 1000 m^{-3}) is 38 times that of the RMT8, the corresponding biomass is 11 times greater. Yet the RMT8 under-sampled copepod juveniles to a greater degree than the adults. The juvenile copepods contributed significantly to the total RMT1 copepod density, but little in the way of biomass.

Distribution

The copepod community distribution (all four species and 'all life stages') is described in the present study by the separation of a neritic and an oceanic group at approximately 67°S. This latitudinal zonation agrees with previous studies

Table VI. Average abundances (ind. 1000 m^{-3}) of the four species in both the Indian and Atlantic sectors of the Southern Ocean.

	Prydz Bay							Croker Passage	South Georgia	Weddell Sea	
	(Jan-Feb)[1]	(Jan-Feb)[2]	(Jan-Feb)[3]	(Sep-Nov)[4]	(Dec)[5]	(Feb)[6]	(Jan-Feb)[7]	(Mar-April)[8]	(Nov-Dec)[9]	(Feb-Mar)[10]	(Feb)[11]
Mesh size (μm)	300	4500	4500	4500	330	50	355	162	330	320	500
Sampling depth (m)	0-200	0-200	0-200	0-200	0-100	0-220	0-1000	0-1000	0-250	0-300	0-200
Calanoides acutus	874	11	72	17	4290	225400	5880	1010	7700	1314+	260
Calanus propinquus	127	8	37	1	1000	11110	880	50	152	676+	263
Rhincalanus gigas	100	15	8	99	3850	250	3010	40	1800	59	37
Metridia gerlachei	250	1	16	4	550	10005	19060	15154*	4052	641	

*included *Metridia lucens* +C-IV to C-VI only

[1]this study; [2]Hosie *et al.* (1997); [3]Hosie & Cochran (1994); [4]Hosie & Stolp (1989); [5]Yamada & Kawamura (1986); [6]Zmijewska (1983); [7]Budnichencko & Khromov (1988); [8]Hopkins (1985); [9]Atkinson (1989b); [10]Boysen-Ennen & Piatkowski (1988); [11]Hubold & Hempel (1987)

in this region (Budnichenko & Khromov 1988, Hosie 1994a) and is associated with the continental shelf edge. This pattern was also described by Hosie *et al.* (in press) who reports the mesoscale distribution of the copepod community based on the catch from the RMT8 net during the same survey in relation to the distribution of zooplankton communities. The present study complements that of Hosie *et al.* (1997) by providing more accurate information on the individual species abundance and distribution within the copepod community. The general pattern of very cold water south of the continental shelf edge and warmer stratified water masses north of the shelf break seen in the present study has also been noted in previous studies (Hosie 1994a, Nunes Vaz & Lennon 1996). This pattern, in association with the circulation of water on and off the continental shelf, might act as an ecological boundary separating continental shelf populations and offshore communities (Brandt & Wadley 1981, Goffart & Hecq 1993).

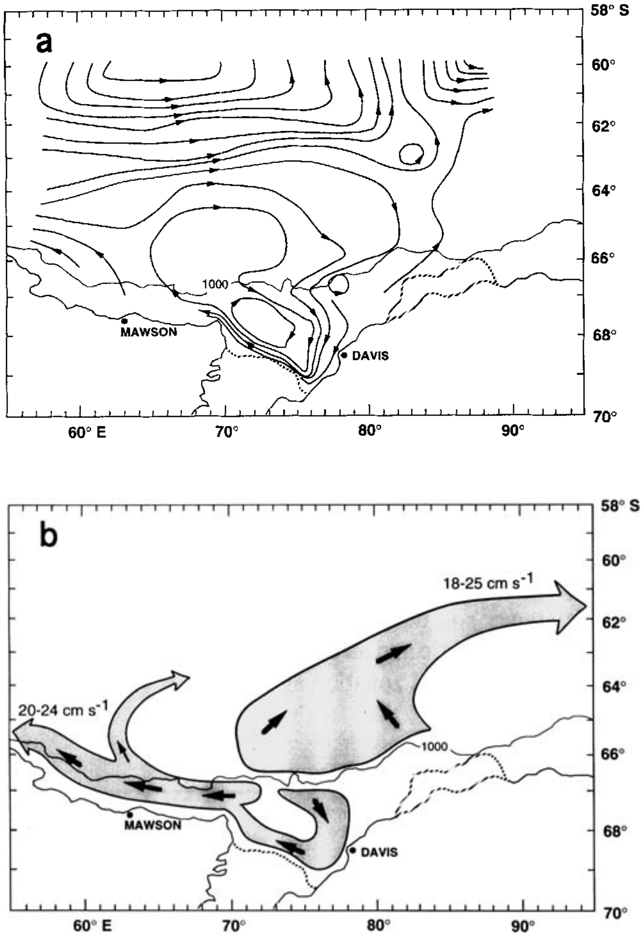


Fig. 11. Horizontal water circulation patterns in the Prydz Bay region. **a.** the geostrophic water flow redrawn from the geopotential anomaly contours of Nunes Vaz & Lennon (in press), **b.** apparent dispersal routes of euphausiid larvae, likely to affect zooplankton distributions, determined from sea-ice buoy and iceberg trajectories, current meters and geostrophic flow. Current speeds shown were determined from iceberg trajectories. (From Hosie 1991).

The inshore region is characterized by low abundance of all copepod species, and particularly of juveniles. Associated with this region is the central part of the gyre which contributes to a well mixed water column (Fig. 11a). Atkinson & Peck (1990) and Hopkins & Torres (1988) likewise found low copepod abundance associated with gyres in the Atlantic sector. The long residence time of water within the gyre means that copepods can complete their life-cycles within the gyre and therefore abundance is primarily a function of the annual primary productivity of the area (Hopkins & Torres 1988), and the number of predators entering the gyre. Given the well mixed conditions, it is likely that the water column would be oligotrophic for a large part of the year which could contribute to low numbers of copepods.

Apart from the neritic and oceanic groups two other groups, each consisting of three stations, are present in the community distribution. Group 4 is characterized by poor species abundance and is located in the centre of the Bay. Group 2 in the north west of the study site represents a high concentration of *R. gigas* which is a dominant offshore species.

Figures 5 & 6 show *C. acutus* and *C. propinquus* in greatest abundance in the north-east of the sampling area which corresponds to the eastern part of the gyre. Hosie & Cochran (1994) likewise found copepods concentrated in this area and suggested that the southward flow of the returning arm of the gyre may bring a higher concentration of copepods from the north. A further hydrographic influence might be the north-east current in this area (Fig. 11b), which Hosie (1994a) identifies as a possible dispersal route for krill larvae as well as a region of high copepod concentration. The distribution of *R. gigas* is clearly offshore as marked by the shelf break (Fig. 4), indicating the species' preference for warmer oceanic waters. While juveniles of *M. gerlachei* are most common near the coast, the species is distributed both inshore and offshore (Fig. 7), confirming the findings of Hosie *et al.* (1997) that the species represents the neritic group as well as the oceanic group.

The adult distribution is identical to that of the 'all life stages' (Fig. 8b) indicating that the late copepodite stages influence the distribution of the community as a whole. Juveniles show inshore and offshore grouping; however, an additional group is seen further south near the coast containing a high abundance of *M. gerlachei* and *C. acutus* juveniles. Zmijewska (1983) also found juveniles of the dominant copepod species distributed further south than the adults. Examination of the Northern Ice Limit charts (Navy-NOAA Joint Ice Center, Naval Polar Oceanography Center, Suitland) for December shows 1–3/10 ice cover near the coast indicating that the annual polynya was present and it persisted over the next few weeks into January 1993. This annual polynya is reported to start in the south of Prydz Bay in December and melts outward to the north to meet the southward receding ice edge. Biological activity therefore begins earlier inshore while the adjacent waters are still covered by ice. This phenomenon is known as the 'oasis effect' and has previously been linked to the occurrence of krill larvae in the south of Prydz Bay (Hosie & Cochran 1994). Therefore we suggest the distribution of juvenile copepods inshore might also be related to this effect.

Species associations

Among the four copepod species, the distributions of *R. gigas* and *M. gerlachei* are discrete, while the distributions of *C. acutus* and *C. propinquus* overlap. Bathmann *et al.* (1993) found latitudinal separation with *R. gigas* being scarce in the vicinity of the continent while *C. acutus* and *C. propinquus* were in equal abundance in the Weddell gyre. We found that temperature appeared to be the most likely controlling factor influencing the species' large-scale distributions, but probably a combination of physical influences, coupled with individual life-cycles contributes to their distributions.

Like Hosie (1994b) we found the adult and larval krill distributions are distinct from that of the copepods. This finding is different to that of Schnack *et al.* (1985), in the Antarctic Peninsula region, who found the distribution of krill larvae to overlap with that of the copepods and suggested that due to their similar feeding behaviour they could be considered as competitors.

The distinct separation of krill and copepod distributions suggests either external control of population density by predation, or internal population control by:

1) niche separation due to direct competition between species, or
2) an independent response of species to the structure of their environment (Bradley & Bradley 1985).

Environmental parameters

Mean temperature is the only environmental parameter that is significantly correlated with copepod distribution, accounting for 34% of the variation. This is slightly less than in previous years where temperature accounted for 52% (Hosie & Cochran 1994) and 49% (Hosie *et al.* 1997) of the variation in zooplankton distribution. Nonetheless, temperature still appears to be the controlling factor which affects the distribution of individual species and thereby species composition in the neritic and oceanic regions.

Mean isotherms plotted in Fig. 2 show a warm intrusion of water in the north-west of the sampling area which corresponds with the geographical location of Group 2 in Fig. 8b, containing a high abundance of *R. gigas*. This was the only species that showed a significant positive correlation with mean temperature, which concurs with the finding by Hosie *et al.* (1997).

Temperature can also affect the community distribution by affecting the formation and dynamics of sea ice. *R. gigas* is the only species which shows a significant correlation with both temperature and ice recession. This species appears to prefer warmer waters which form when cleared of ice via surface heating (Zmijewska 1983, Hubold *et al.* 1988, Atkinson *et al.* 1990).

In polar regions large variations in salinity can occur due to ejection of salt in ice formation (in winter) and the dilution of surface waters by ice melt (in summer) (Garrison *et al.* 1986). Mean salinity however, is not significantly correlated with the pattern of distribution. Hosie *et al.* (1997) found mean salinity to be significant in explaining just 13.7% of the variation in the zooplankton community distribution. Likewise, previous studies have found salinity to have little effect on copepod distribution (Hosie 1994a, Hosie & Cochran 1994).

Phytoplankton, as represented by chl *a* concentration, is not as significantly correlated with the copepod community distribution in the present study compared to previous years (Hosie 1994a). Only *C. propinquus* and adults of *C. acutus* show a significant negative correlation with integrated, surface and peak chl *a* indicating that these copepods are either actively avoiding the phytoplankton, unlikely for herbivores, or that they have reduced the phytoplankton concentration by grazing. Alternatively, the patterns may be unrelated with the inshore phytoplankton blooms coinciding with the low abundance region of some of the species. This low abundance may be more related to an environmental effect (e.g. temperature), rather than a food effect.

That zooplankton distribution is uncoupled from that of the phytoplankton has been widely reported. In general, the phytoplankton bloom in the Southern Ocean is described as situated more southerly than the summer belt of zooplankton biomass (Hardy 1936, Hardy & Gunther 1936, Voronina 1978). A more recent hypothesis is that initial spring copepod reproduction is probably fuelled by internal lipid reserves in all species, rather than by the onset of phytoplankton blooms (Hagen & Schnack-Schiel 1996).

Acknowledgements

We are grateful to the captain and crew of the RSV *Aurora Australis* for their interest and assistance, and to the following for their assistance in the collection and on board processing of samples: M. Stolp, M. Sands, P. Virtue, H.J. Marchant and R. Burbury. We thank Ms Kerrie Swadling, Dr Angus Atkinson, Dr Atsushi Tanimura and an anonymous reviewer for improving the manuscript.

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